

THE POLLEN MORPHOLOGY OF THE NATIVE NEW ENGLAND SPECIES OF THE GENUS¹ ACER (ACERACEAE)

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ABSTRACT

Detailed descriptions.

The pollen morphology of the seven species of maple (genus *Acer*, family Aceraceae) indigenous to New England is described. The species included are *Acer pensylvanicum* L., *A. rubrum* L., *A. spicatum* Lam., *A. negundo* L., *A. saccharinum* L., *A. nigrum* Michx. f., and *A. saccharum* Marsh. Detailed descriptions for the species are based on both scanning electron and light microscope observations. The morphological characteristics and classification of the pollen grains of the New England species are discussed in comparison with the observations of previous workers. Size ranges, Polar axis/Equatorial axis ratios (P/E), and Polar Area indices are summarized. Photomicrographs from both light and scanning electron microscopes are included for each species.

Key words: palynology, pollen morphology, Aceraceae, *Acer*, Maple, *Acer pensylvanicum*, *A. rubrum*, *A. spicatum*, *A. negundo*, *A. saccharinum*, *A. saccharum*, *A. nigrum*.

The purpose of this paper is to provide detailed descriptions, based on observations made with both the light microscope and the scanning electron microscope, that will aid in the identification of pollen of the seven species of the genus *Acer* (Aceraceae, Maple family) native to New England. The descriptions, light micrographs, and scanning electron micrographs presented here should be of value to workers in the various fields of palynology in New England and elsewhere.

Acer, a genus of nearly 150 woody species, is found chiefly in the temperate regions of the northern hemisphere (Brizicky, 1963). Of the 15 species native to the United States (Lawrence, 1951), seven are indigenous to the New England region: *Acer negundo* L. (Boxelder), *A. nigrum* Michx. f. (Black Maple), *A. pensylvanicum* L. (Striped Maple), *A. rubrum* L. (Red Maple), *A. saccharinum* L. (Silver Maple), *A. saccharum* Marsh. (Sugar Maple), and *A. spicatum* Lam. (Mountain Maple). Several of these species are significant

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components of the region's forests. Certain introduced species, such as *A. platanoides* L. (Norway Maple) and *A. pseudo-platanus* L. (Planetree or Sycamore Maple), are also occasionally found escaped from cultivation in this region.

The species examined in the present study, with the exception of *Acer negundo* which is anemophilous, are reported to be amphiphilous. That is, they are capable of effecting pollination through either anemophilous or entomophilous means (Wodehouse, 1935, 1945; Hesse, 1979). Field observations in New England indicate an apparent tendency toward anemophily in several species (*A. rubrum*, *A. saccharinum*, *A. saccharum*). This tendency is suggested by both a characteristic flowering period, which occurs well before the emergence of the leaves in the spring, and the exsertion of the anthers well beyond the perianth, exposing the dehiscing anthers to the wind. As a result of this tendency, these species contribute to the airborne pollen rain during their peak periods of flowering, and may be a contributing factor in the cause of early spring "hay fever." The anemophilous condition also explains why grains of several species of this genus are frequently encountered in the analysis of sediments (Davis, 1965). It is reported by Sangster and Dale (1964), however, that *Acer* grains are under-represented in sediments under experimental conditions, a phenomenon which they attribute to rapid decomposition.

Most of the previous studies of pollen morphology in the genus *Acer* have been based on light microscope observations. Wodehouse (1935), Erdtman (1952), Erdtman, Berglund and Praglowski (1961), and Praglowski (1962), each provide basic morphological information for a few species of the genus. A more thorough light microscope study was conducted by Helmich (1963), who provides a key to eighteen, and illustrations of nine, North American species, as an aid toward the identification of *Acer* pollen in Cenozoic sediments. Another study designed to aid in the analysis of fossil *Acer* pollen is that of Gogichaishvili (1964), who describes and illustrates eleven species of *Acer* native to the Caucasus of Russia.

Several recent studies have involved scanning electron microscopy as well as light microscope observations. Biesboer (1975) published a survey of the pollen morphology of 40 taxa in the genus *Acer* and one species of the related genus *Dipteronia*. He was able to recognize four distinct pollen types, based on the visible sculpturing patterns of the pollen grain surface. He designated these simply as Types I - striate,

II -rugulose, III - granular, and IV - microreticulate. Clarke and Jones (1978) adopt Biesboer's Types for the grains which they describe and illustrate in their study of the pollen of five species of *Acer* which occur naturally in northwestern Europe. Hesse (1979), studying the same northwest European species, considers the ultrastructure of the pollen grain wall and the distribution of pollenkit on the wall surfaces in relation to pollen stickiness and its relationship to wind- and insect-pollination.

Based on morphological characteristics of their pollen the seven species included in this study can be assigned to three of the four Types established by Biesboer (1975): Type I-striate, II-rugulose, and IV-microreticulate. Type III-granular is not represented among our species.

MATERIALS AND METHODS

Material for this study was obtained from specimens in the Gray Herbarium (GH); the New England Botanical Club Herbarium (NEBC); and the Hodgdon Herbarium (NHA). Voucher information is cited with the description of each species.

Material for light microscopy was acetolyzed (Faegri & Iversen, 1975), washed in two rinses of distilled water and transferred to glycerine jelly in small storage vials. Acetolyzed grains were also dehydrated in xylene, transferred to silicone oil (2000 centistokes viscosity) and kept in small storage vials. Microscope slides were later made from the stored material.

Glycerine jelly (g.j.) was chosen as a mounting medium for this study because it provides a simple yet relatively permanent mounting medium which is widely used in palynology. However, pollen grains are known to expand in this medium, affecting their shape and dimensions. In order to assess the effects of g.j. on grains of *Acer*, silicone oil (s.o.) was used as an alternative mounting medium. This was accomplished by mounting grains from one population of each species in s.o. as well as g.j. The separate measurements were then compared. It should be noted that, in each case, upon comparison of s.o. versus g.j. measurements, significant differences were always encountered regarding both the P/E ratios and polar area indices.

The principal measurements presented in the descriptions below were taken from grains embedded in glycerine jelly. Separate average polar and equatorial axes, (P/E ratios, see Erdtman, 1952) and polar

area indices (P.A.I.) (See Figs. I and II) were calculated based on measurements of 30 grains from each population. In order to allow the grains to respond to the g.j. medium, measurements were taken approximately two weeks after embedding. Measurements were

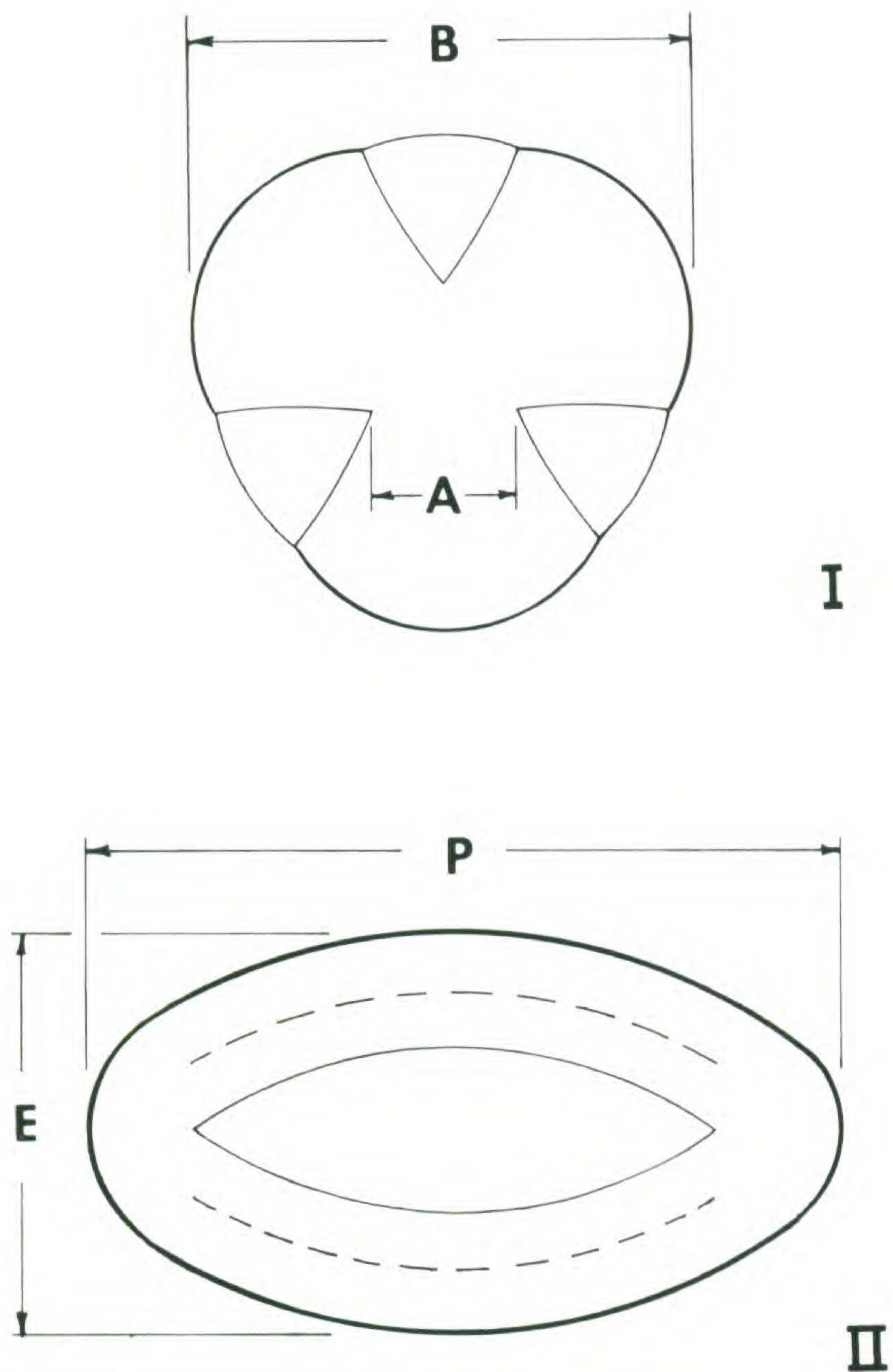


Figure I & II. I. Polar Area Index: Calculated as the ratio of the largest distance between the ends of two furrows (A) and the greatest diameter of the pollen grain (B). II. Polar axis/Equatorial axis ratio (P/E ratio); Calculated as the ratio between the polar axis length (P) and the equatorial axis length (E).

taken on an AO series 20 Microstar brightfield microscope, at 1000 $\times$. The measurements from silicone oil preparations are included in parentheses for each species.

For scanning electron microscopy, dried anthers were removed from specimens and acetolyzed (Faegri & Iversen, 1975). After the second distilled water wash, the material was washed in two successive 100% acetone washes, the first for ten minutes and the second for 30 minutes. The pollen material was then transferred to aluminum stubs, using a Pasteur pipette. The stubs had been previously coated with an acetone-tape adhesive (1mm of half-inch double-stick tape partially dissolved in 10 ml of 100% acetone). The stubs were then coated with palladium-gold on a TECHNICS 2 sputter coater and examined with an AMR 1000 Scanning Electron Microscope at the Museum of Comparative Zoology of Harvard University.

Unless otherwise noted the terminology of Erdtman (1952) is used in our descriptions. The species are grouped according to the types established by Biesboer (outlined above), based on patterns of sexine sculpturing.

GENERAL GRAIN DESCRIPTION

Grains tricolpate (tricolporate in *Acer spicatum*), radially symmetrical, isopolar, colpi long and narrow reaching nearly to the poles, margo absent, colpus membranes granular. Overall grain shape ranging from suboblate to prolate. Exine thickness (measured in Amb view) ca. 1.0 μm , thickest in center of mesocolpium thinning slightly toward colpi; bacula present; sexine tectate in two species and semitectate (Faegri & Iversen, 1975) in five species; sexine striate, rugulate (Faegri & Iversen, 1975), microreticulate or striato-reticulate.

TYPE I: STRIATE

***Acer pensylvanicum*:** (Figures 3 & 7) lirae and striae appearing equal in width, or nearly so, fairly uniform in width throughout their length, variously arranged in relation to the polar axis, similar in mesocolpium and apocolpium; sexine semitectate, exine thickness ca. 1.0 μm . Measurements: Ossipee, NH (*Philbrick 473*), P/E ratio, range 1.11 – 1.48, mean 1.30 ± 0.10 ; P.A.I., range 0.148 – 0.269, mean 0.209 ± 0.04 . (s.o.: P/E ratio, range 0.96 – 1.39, mean 1.09 ± 0.08 ;

P.A.I., range 0.136 – 0.820, mean 0.243 ± 0.12). Cape Elizabeth, Me. (*Moulton s.n.*), P/E ratio, range 1.12 – 1.47, mean 1.22 ± 0.08 ; P.A.I., range 0.102 – 0.233, mean 0.163 ± 0.04 . Southington, Conn. (*Bissell s.n.*), P/E ratio, range 0.88 – 1.66, mean 1.19 ± 0.13 ; P.A.I., range 0.080 – 0.235, mean 0.143 ± 0.05 . Rutland, VT (*Eggleston s.n.*), P/E ratio, range 1.07 – 1.45, mean 1.29 ± 0.22 ; P.A.I., range 0.121 – 0.241, mean 0.176 ± 0.03 .

Voucher material: *Philbrick 473*, 21 May 1978, (NHA); *Moulton s.n.*, 27 May 1905 (NHA); *Kennedy s.n.*, 15 May 1901 (GH); *Bissell s.n.*, 18 May 1898 (GH); *Eggleston s.n.*, 16 May 1897 (GH).

Acer rubrum: (Figures 3 & 8) lirae and striae variable in width, not uniform throughout their length, variously arranged in relation to polar axis, lirae usually wider than striae; sculpturing similar in mesocolpium and apocolpium; lirae appearing interconnected, thus forming a more or less continuous striate network throughout the grain length, sexine semitectate, exine thickness ca. $1.0 \mu\text{m}$. Measurements: Durham, NH (*Philbrick 377*), P/E ratio, range 0.89 – 1.40, mean 1.42 ± 0.12 ; P.A.I., range 0.119 – 0.256, mean 0.163 ± 0.04 . (s.o.: P/E ratio, range 0.77 – 1.04, mean 0.92 ± 0.07 ; P.A.I., range 0.103 – 0.233, mean $0.181 \pm .03$). Gray County, Me. (*Fellows 1416*), P/E ratio, range 1.10 – 1.52, mean 1.33 ± 0.12 ; P.A.I., range 0.092 – 0.166, mean 0.126 ± 0.02 . Sunderland, Ma. (*Floyd s.n.*), P/E ratio, range 1.21 – 1.63, mean 1.47 ± 0.10 ; P.A.I., range 0.055 – 0.122, mean 0.102 ± 0.02 .

Voucher material; *Philbrick 377*, 23 April 1978 (NHA); *Fellows 1416*, 22 April 1900 (NHA); *Floyd s.n.*, 17 April 1915 (NEBC).

Acer spicatum: (Figures 4, 9, & 10) grains tricolporate, the pores made up of an inner and outer rim; mean pore size $4.2 \mu\text{m}$ (measured along the polar axis in the equatorial view); lirae and striae on most grains visible only in the peripheral regions at mid focus; when visible the lirae are wider than the striae. As a result of this semitransparent nature of the sexine the bacula become visible, causing the surface of the grain to appear granular; sexine tectate, exine thickness ca. $1.0 \mu\text{m}$. Measurements: Isle au Haut, Me. (*Wise 38*), P/E ratio, range 1.04 – 1.44, mean 1.26 ± 0.11 ; P.A.I., range 0.120 – 0.263, mean 0.216 ± 0.04 . Pownal, VT (*Kennedy s.n.*), P/E ratio, range 1.09 – 1.41, mean 1.24 ± 0.09 ; P.A.I., range 0.150 – 0.285, mean 0.209 ± 0.03 . Berkshire Co., MA. (*Walters s.n.*), P/E ratio, range 1.05 – 1.47, mean 1.27 ± 0.10 ;

P.A.I., range 0.125 – 0.273, mean 0.183 ± 0.03 . Southington, Conn. (*Bissell s.n.*), P/E ratio, range 1.14 – 1.50, mean 1.27 ± 0.08 ; P.A.I., range 0.136 – 0.286, mean 0.190 ± 0.04 . Wolfeboro, NH (*Sargent s.n.*), P/E ratio, range 0.81 – 1.42, mean 1.28 ± 0.11 ; P.A.I., range 0.125 – 0.231, mean 0.175 ± 0.03 . (s.o.: P/E ratio, range 1.11 – 1.43, mean 1.22 ± 0.09 ; P.A.I.; range 0.111 – 0.235, mean 0.173 ± 0.04).

Voucher material: *Wise* 38, 5 July 1968 (NHA); *Walters s.n.*, 8 June 1913 (NHA); *Sargent s.n.*, 6 June 1918 (NHA); *Kennedy s.n.*, 17 June 1901 (GH); *Bissell s.n.*, 30 May 1901 (GH).

TYPE II: RUGULOSE (=rugulate)

Acer negundo: (Figures 4, 5, & 11) sexine rugulate, rugulae irregularly arranged, up to $4 \mu\text{m}$ in length, similar in mesocolpium and apocolpium; sexine appears “patchy” at low focus, these patchy areas are up to $3 \mu\text{m}$ in width; sexine tectate, exine thickness ca. $1.0 \mu\text{m}$. Measurements: Durham, NH (*Philbrick 401*), P/E ratio, range 0.93 – 1.63, mean 1.24 ± 0.17 ; P.A.I., 0.250 – 0.414, mean 0.334 ± 0.05 . (s.o.: P/E ratio, range 0.88 – 1.12, mean 1.02 ± 0.06 ; P.A.I., range 0.269 – 0.435, mean 0.361 ± 0.04). Burlington, VT (*Pringle s.n.*), P/E ratio, range 1.18 – 1.46, mean 1.32 ± 0.08 , P.A.I.; range 0.094 – 0.258, mean 0.185 ± 0.04 . New Milford, Conn. (*Averill s.n.*), P/E ratio, range 1.00 – 1.43, mean 1.25 ± 0.10 ; P.A.I., range 0.138 – 0.276, mean 0.215 ± 0.04 . Dorchester, MA (*Jenks s.n.*), P/E ratio, range 1.19 – 1.62, mean 1.38 ± 0.13 ; P.A.I., range 0.125 – 0.233, mean 0.174 ± 0.02 .

Voucher material; *Philbrick 401*, 1 May 1978 (NHA); *Pringle s.n.*, 13 May 1879 (GH); *Jenks s.n.*, 1883 (NEBC); *Averill s.n.*, 19 April 1897 (NEBC).

Acer saccharinum: (Figures 5 & 12) sexine rugulate, rugulae irregularly arranged, less than $2 \mu\text{m}$ in length, much finer in appearance than those of *A. negundo*; rugulae slightly smaller in apocolpium versus mesocolpium; at low focus “patchy” dark areas, if present, less than $1 \mu\text{m}$ in width; sexine tectate; exine thickness ca. $1.0 \mu\text{m}$. Measurements: Durham, NH (*Philbrick 350*), P/E ratio, range 1.19 – 1.48, mean 1.31 ± 0.08 ; P.A.I., range 0.108 – 0.243, mean 0.174 ± 0.03 . (s.o.: P/E ratio, range 0.860 – 1.28, mean 1.04 ± 0.09 ; P.A.I., range 0.140 – 0.280, mean 0.195 ± 0.03). Rutland, VT (*Eggleston s.n.*), P/E ratio, range 1.00 – 1.55, mean 1.35 ± 0.14 ; P.A.I., range 0.102 – 0.294, mean 0.185 ± 0.04 . Providence, RI (*Hope 483*), P/E

ratio, range 1.05 – 1.40, mean 1.24 ± 0.08 ; P.A.I., range 0.097 – 0.179, mean 0.136 ± 0.02 .

Voucher material: *Philbrick* 350, 29 March 1978 (NHA), *Eggleston s.n.*, 20 April 1895 (GH); *Hope* 483, 13 March 1910 (NEBC).

TYPE IV: MICRORETICULATE

Biesboer places both *Acer saccharum* and *A. nigrum* in his Type IV grouping, which is characterized as having a microreticulate sexine. Our material of *A. saccharum* does not seem to fall very neatly into this group, since its sexine appears to be more striato-reticulate, an intermediate condition between striate and reticulate. The reticulate pattern appears at a lower level, with the striae situated above the reticulum. Therefore, two separate networks are formed, an upper striate network and a lower microreticulate network. However, we retain *A. saccharum* in the Type IV group because Biesboer expands this group to include *A. saccharum* ssp. *grandidentatum*, which he reports may occasionally be striato-reticulate. *Acer nigrum* also exhibits this striato-reticulate character, but to a much more limited extent.

Acer saccharum: (Figures 5 & 13) sexine striato-reticulate in mesocolpium; striate sculpturing occurring above the microreticulate sculpturing; sexine tending toward microreticulate in apocolpium; sexine semitectate; exine thickness ca. $1.0 \mu\text{m}$. Measurements: Durham, NH (*Philbrick* 425), P/E ratio, range 0.97 – 1.33, mean 1.16 ± 0.09 ; P.A.I., range 0.025 – 0.457, mean 0.184 ± 0.07 . (s.o.: P/E ratio, range 0.890 – 1.43, mean 1.12 ± 0.12 ; P.A.I., range 0.172 – 0.250, mean 0.194 ± 0.03 .) Franklin, Conn. (*Woodward s.n.*), P/E ratio, range 1.05 – 1.56, mean 1.30 ± 0.12 ; P.A.I., none available. South Chesterville, ME (*Eaton s.n.*), P/E ratio, range 1.19 – 1.64, mean 1.40 ± 0.11 ; P.A.I., range 0.096 – 0.258, mean 0.167 ± 0.04 . Amherst, MA (*Rogers s.n.*), P/E ratio, range 1.22 – 1.55, mean 1.35 ± 0.08 ; P.A.I., range 0.086 – 0.194, mean 0.135 ± 0.02 .

Voucher material: *Philbrick* 425, 10 May 1978 (NHA); *Rogers s.n.*, 22 May 1950 (NHA); *Eaton s.n.*, May 1897 (NHA); *Woodward s.n.*, 2, 4 May 1905 (NEBC).

Acer nigrum: (Figures 6 & 14) sexine microreticulate, frequently tending toward striato-reticulate (the striato-reticulate nature is less

pronounced in this species than in *A. saccharum*); sexine semitectate; exine thickness ca. $1.0\ \mu\text{m}$. Measurements: western VT (*Pringle s.n.*), P/E ratio, range $1.17 - 1.61$, mean 1.41 ± 0.10 ; P.A.I., range $0.128 - 0.244$, mean 0.182 ± 0.03 . (s.o.: P/E ratio, range $0.91 - 1.41$, mean 1.15 ± 0.15 ; P.A.I., range $0.125 - 0.300$, mean 0.191 ± 0.04).

Voucher material: *Pringle s.n.*, 27 May 1879 (NEBC).

DISCUSSION

Grains from the seven New England species included in this study fall into three of the four morphological types, based on sexine sculpturing, established by Biesboer (1975). *Acer pensylvanicum*, *A. rubrum*, and *A. spicatum* conform to Biesboer's Type I, striate group. All three species have a sculptured sexine differentiated into lirae and striae, with no significant difference in the sculpturing between the mesocolpium and apocolpium regions of the grain.

When viewed under the light microscope (Figure 3, A-D), at $1000\times$, the lirae of *Acer pensylvanicum* are observed to be fairly uniform in width though discontinuous, that is, they occur as segments of various lengths. The scanning electron micrographs of this species (Figure 7) illustrate both these characters clearly, showing the uniformity in width and the abrupt terminations of the lirae. The other two species of the striate group, *A. rubrum* and *A. spicatum*, do not exhibit this discontinuous pattern.

The mean P/E ratios for all the populations of *A. pensylvanicum* fall within the subprolate category of Erdtman (1952). However, with the exception of the *Bissell s.n.* population, the P/E ratios for all the populations of this species ranged from prolate-spheroidal to prolate. The *Bissell* population ranged from oblate-spheroidal to prolate.

The second species in the striate group, *Acer rubrum* (Figure 3 E-H, & 8), is characterized by having lirae which are notably wider than are the striae. This species also exhibits lirae and striae which vary in their width in relation to one another throughout the grain surface. Therefore, the uniformity of width noted in *A. pensylvanicum* is lacking in *A. rubrum*. The lirae of *A. rubrum* appear interconnected, thus forming a continuous network of lirae throughout the length of the grain. This network is also apparent in our scanning electron micrographs of *A. spicatum* (Figures 9 & 10), but not apparent in the light micrographs of this species. *Acer pensylvanicum* (Figure 7) does not show this continuous network.

Two of the three *A. rubrum* populations (*Philbrick 377*, *Floyd s.n.*) are characterized by mean P/E ratios which fall into Erdtman's prolate grouping, the remaining population (*Fellows 1416*) proved to be marginal between subprolate and prolate. The P/E ratios for all three populations of this species ranged over several of Erdtman's shape categories: oblate-spheroidal to prolate (*Philbrick 372*); prolate-spheroidal to prolate (*Fellows s.n.*); subprolate to prolate (*Floyd s.n.*).

When observed with the light microscope the lirae and striae of the third striate species, *Acer spicatum* (Figure 4 A–D), are much less obvious than those of the previous two species. They are observable only in the peripheral regions of the grain where the sexine is in oblique view. As a result of this apparent semitransparent quality of the *A. spicatum* sexine, the bacula subtending the tectum give a pseudo-granular appearance to the surface of the grain. The striate nature is apparent, however, in the scanning electron micrographs of the species (Figures 9 & 10).

All the populations of *A. spicatum* yielded mean P/E ratios within Erdtman's subprolate group. This species was unique in the sense that the ratios from the separate populations displayed no significant differences when compared statistically. The other species of this study shared little, if any, similarity between populations in regard to statistical analysis of P/E ratios.

In terms of tectal structure, two species of the striate group, *Acer pensylvanicum* (Figures 3 A–D, 7) and *A. rubrum* (Figures 3 E–F, 8), show a semitectate condition which is most obvious in the scanning electron micrographs of these species. The other species, *A. spicatum* (Figures 9 & 10), tends more toward a tectate condition, although some areas of the grain do lack a full tectum. The semitectate condition (in the sense of Faegri & Iversen, 1975) observed in these species differs from that described in the comprehensive pollen description of Biesboer (1975), who characterized all three species as having a full tectum.

Pollen grains conforming to Biesboer's rugulose group, Type II, are found in *Acer negundo* and *A. saccharinum*. As a result of its wider use in palynological texts (Faegri & Iversen, 1975, Moore & Webb, 1978), we choose to use the term "rugulate" in place of the less frequently used term "rugulose". Both terms describe the same wrinkled condition. The most prominent feature distinguishing *A. negundo* from *A. saccharinum* is the size and orientation of the

individual rugulae. *Acer negundo* (Figures 4, 5, & 11) possesses rugulae which are much more elongate, up to 4 μ m in length, and more variable in shape than those of *A. saccharinum* (Figures 5 & 12), with rugulae which are more uniform in shape and less than 2 μ m in length. Another character which separates the two species is the presence or absence of dark "patchy" areas, apparent while focusing down through the rugulae. *Acer negundo* (see arrow, Figure 5A) exhibits these dark areas, which are up to 4 μ m in width, while in *A. saccharinum* the areas are less than 1 μ m in width if they are present at all. Both rugulate species exhibit larger rugulae in the mesocolpium region than in the apocolpium region.

Two populations of *A. saccharinum* (Philbrick 350, Hope 483) have mean P/E ratios which fall within Erdtman's subprolate category, with the remaining population (Eggleston s.n.) in the prolate group. As is commonly found among the species covered, the range of P/E ratios for this species extends through several of Erdtman's categories, Philbrick 350 extended from subprolate through prolate, with both the Eggleston s.n. and Hope 483 populations ranging from prolate-spheroidal to prolate.

Three populations of *A. negundo* (Philbrick 401, Pringle s.n., Averill s.n.) possess mean P/E ratios which are included in the subprolate group. The remaining population (Jenks s.n.) falls within the prolate category. In this species P/E ratios range from subprolate to prolate in Jenks s.n. and Pringle s.n., oblate-spheroidal to prolate in Philbrick 401 and prolate-spheroidal to prolate in the Averill s.n. material.

Two of our species, *Acer nigrum* and *A. saccharum*, exhibit pollen grains that can be attributed to Biesboer's microreticulate group, Type IV. However, we observed a striato-reticulate sexine, a condition intermediate between striate and reticulate, to be prominent in *A. saccharum* and common in *A. nigrum*. In *A. saccharum* (Figures 5 G-J & 13) both the striate and microreticulate sculpturings appear to be present, but at different levels in the sexine of the mesocolpium, with a more reticulate condition in the apocolpium. The striate condition is located at an upper level with the microreticulate condition situated beneath the lirae. The latter condition, as seen in the scanning electron micrographs for *A. saccharum* (Figure 13) and *A. nigrum* (Figure 14), is formed by various sized tectal ridges connecting the lirae across the striae.

The mean P/E ratios of the *Philbrick 425* and *Woodward s.n.* populations of *A. saccharum* fall within the subprolate group and the *Eaton s.n.* and *Rogers s.n.* into the prolate category of Erdtman. The upper range of all four populations lies in the prolate group, while the lower ranges of *Eaton s.n.* and *Rogers s.n.* are subprolate, with the *Philbrick 425* being oblate-spheroidal and *Woodward s.n.* being prolate-spheroidal.

Acer nigrum exhibits a sexine which corresponds more closely with Biesboer's description. With the light microscope (Figure 6 A–D) the sexine of this species appears predominantly microreticulate in both the mesocolpium and apocolpium regions, though there are areas on most of the grains which do show a striato-reticulate condition. The one population of *A. nigrum* (*Pringle s.n.*) displayed a mean P/E value falling within Erdtman's prolate grouping, while extremes ranged from the subprolate to prolate categories.

We place *Acer saccharum* in Biesboer's Type IV group inasmuch as Biesboer includes there *A. saccharum* ssp. *grandidentatum*, which he reports to be occasionally striato-reticulate.

None of the seven species studied fall within Biesboer's granular group, Type III. This condition appears to be uncommon in the genus, as illustrated by the fact that only one (*Acer carpinifolium*) of the 41 taxa studied by Biesboer has a granular sexine. However, it should be kept in mind that, as of this writing, data on the pollen morphology of fewer than half the known species of the genus *Acer* can be found in the literature, and detailed descriptions of individual species are even less numerous. Biesboer (1975) provides descriptions of the four general types which he identified among the 41 taxa he examined, rather than descriptions of the individual species. Similarly, Helmich (1963) lists the names of 45 species which she examined, but provides detailed descriptions and a key for only 15 North American species, of which she considers only 13 to be "definite species". The studies of Gogichaishvili (1964), Clarke and Jones (1978), and Hesse (1979) add information for about 12 European or Asian species. Thus, new pollen "types", or additional species with granular exines, may be identified as additional studies appear in the literature.

Although the use of the polar area index is of important diagnostic value in many cases, it proves of little use in distinguishing the different *Acer* species covered here. Regarding this index, in almost every case there are no correlations between species or even similarities between separate populations within the same species.

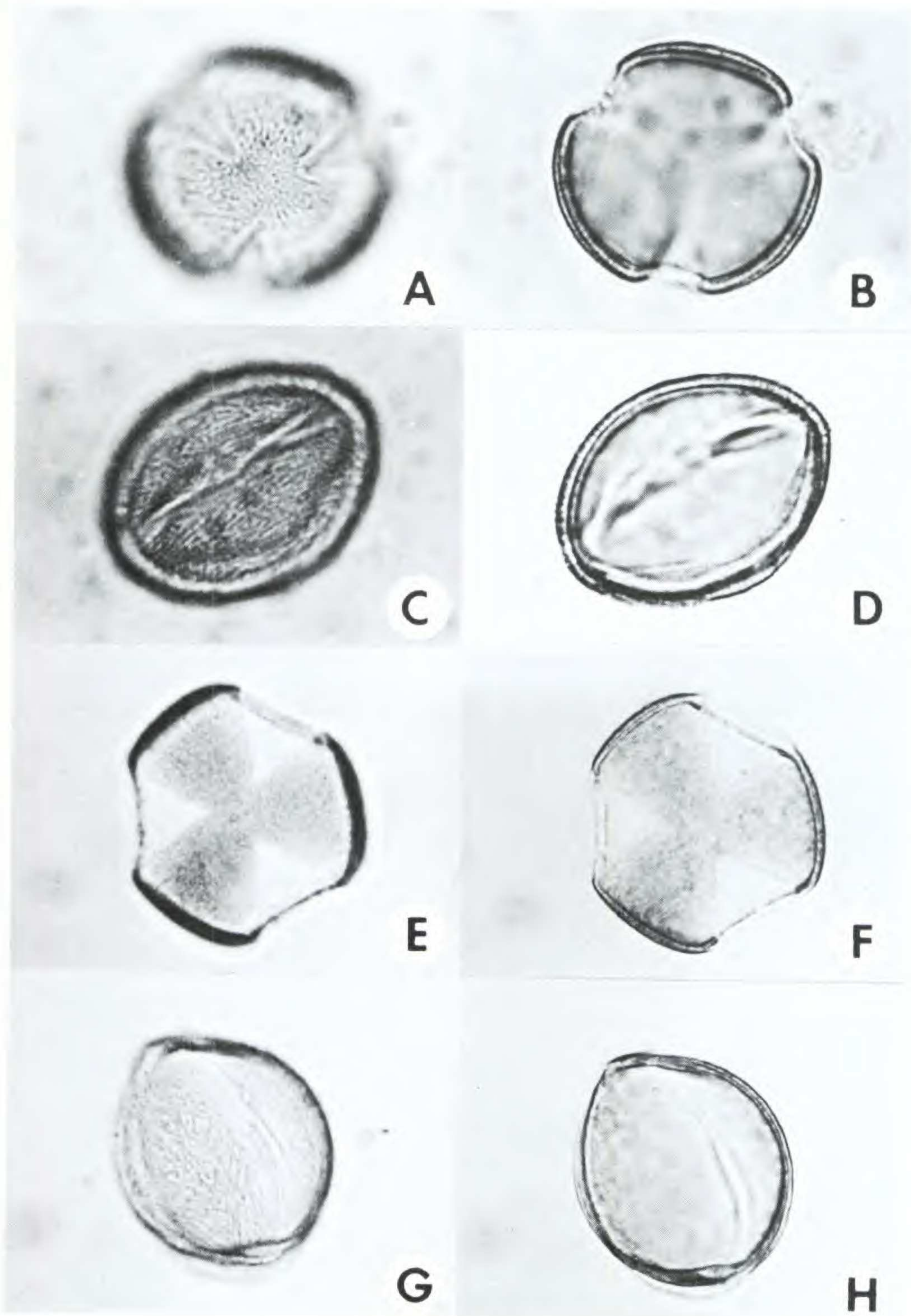


Figure 3. Light micrographs: A-D; *Acer pensylvanicum*: A; Polar view, High focus, 3165X. B; Polar view, Mid focus, 3230X. C; Equatorial view, High focus, 3487X. D; Equatorial view, Mid focus, 3487X. E-H; *A. rubrum*: E; Polar view, High focus, 1343X. F; Polar view, mid focus, 1343X. G; Equatorial view, High focus, 1273X. H; Equatorial view, Mid focus, 1273X.

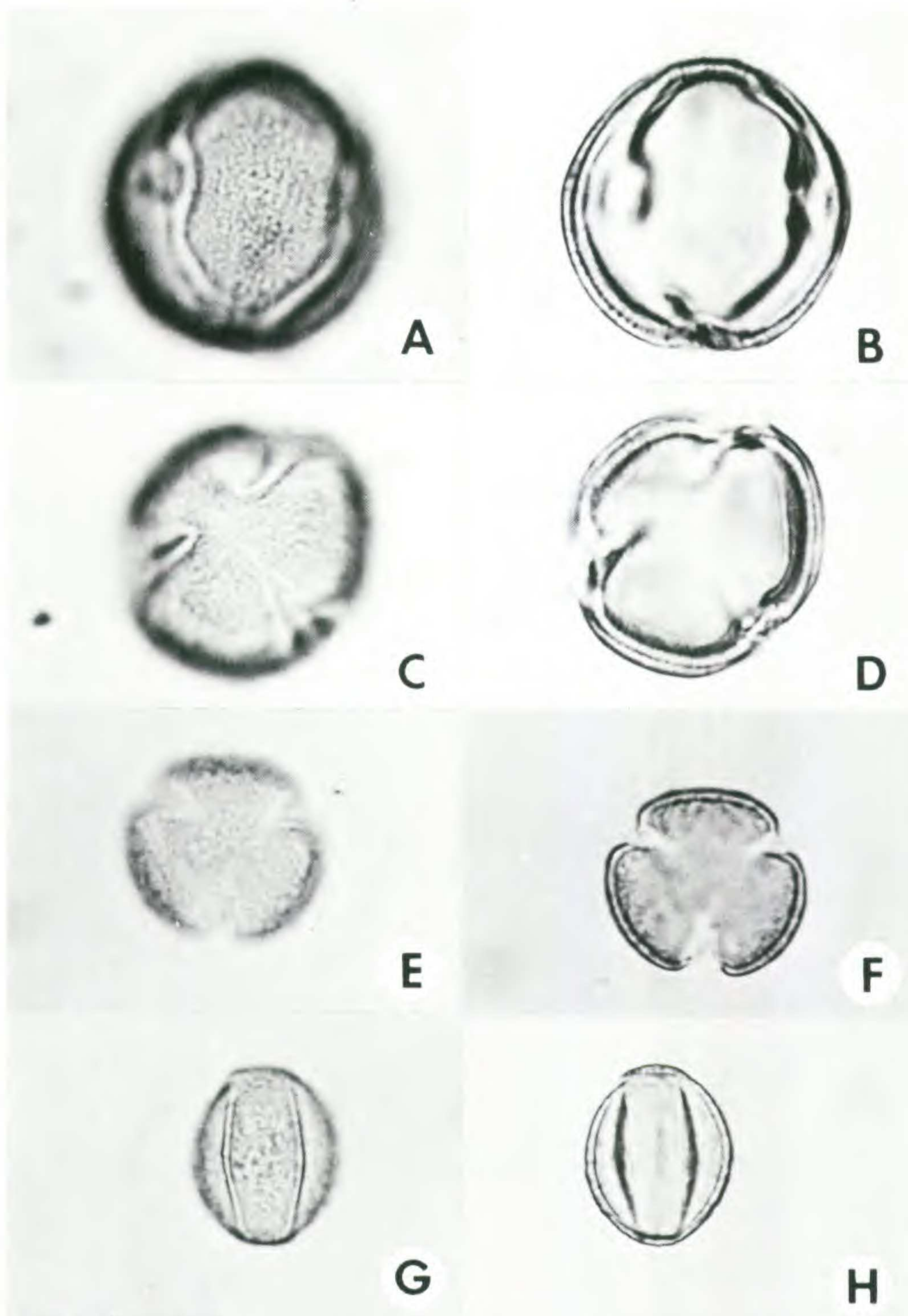


Figure 4. Light micrographs: A-D; *A. spicatum*: A; Equatorial view, High focus, 3429X. B; Equatorial view, Mid focus, 3429X. C; Polar view, High focus, 3230X. D; Polar view, Mid focus, 3230X. E-H; *A. negundo*: E; Polar view, High focus, 1311X. F; Polar view, Mid focus, 1311X. G; Equatorial view, High focus, 1380X; H; Equatorial view, Mid focus, 1380X.

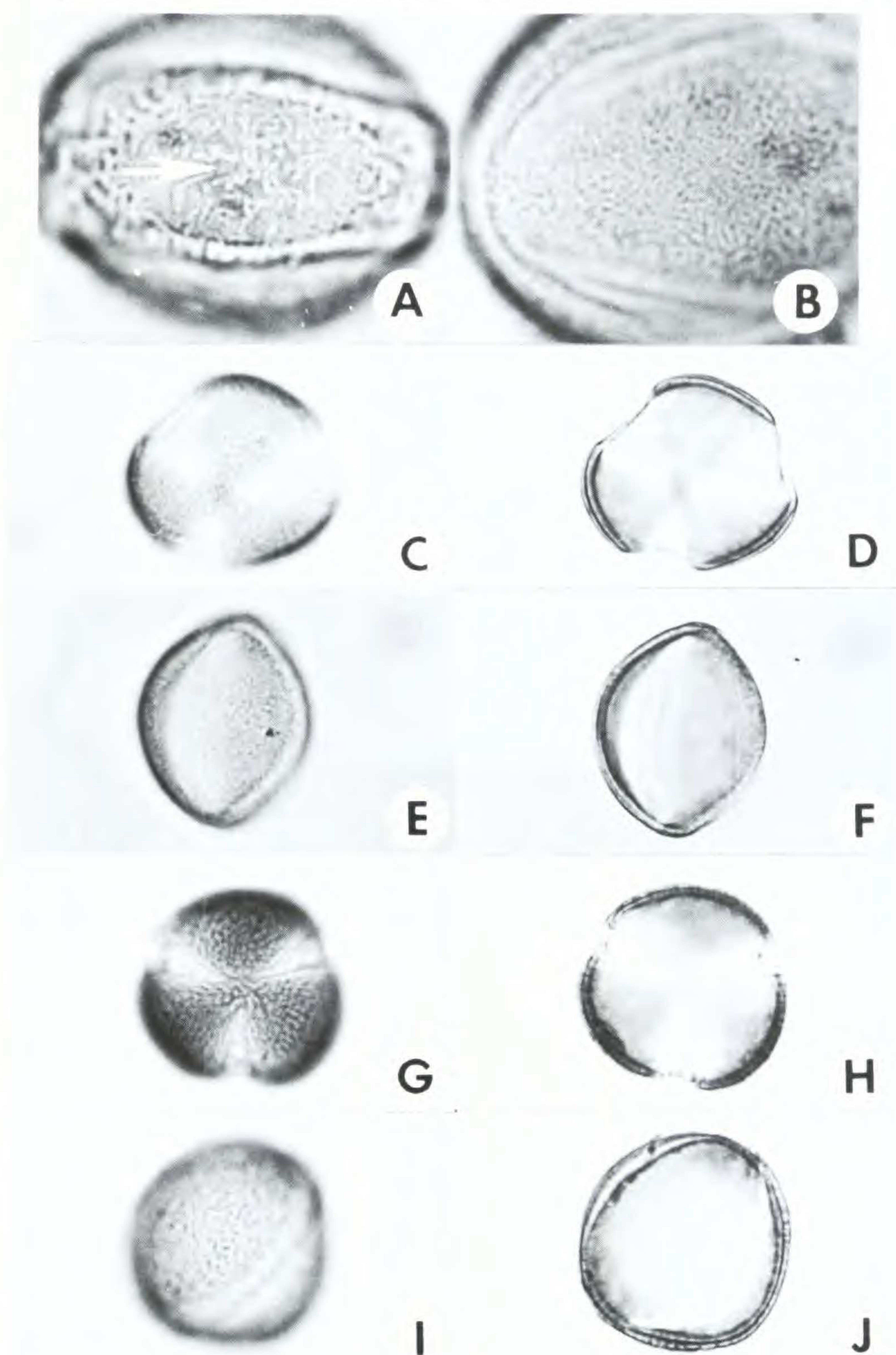


Figure 5. Light micrographs: **A**; *Acer negundo*; Equatorial view, Low focus, showing "patchy" dark areas separating the rugulae, 3128 $\times$. **B–F**; *A. saccharinum*; **B**; Equatorial view, showing smaller and more uniform rugulae than in *A. negundo*, also smaller "patchy" dark areas, 3214 $\times$. **C**; Polar view, High focus, 1200 $\times$. **D**; Polar view, Mid focus, 1200 $\times$. **E**; Equatorial view, High focus, 1257 $\times$. **F**; Equatorial view, Mid focus, 1257 $\times$. **G–J**; *A. saccharum*: **G**; Polar view, High focus, 1328 $\times$. **H**; Polar view, Mid focus, 1328 $\times$. **I**; Equatorial view, High focus, 1267 $\times$. **J**; Equatorial view, Mid focus, 1267 $\times$.

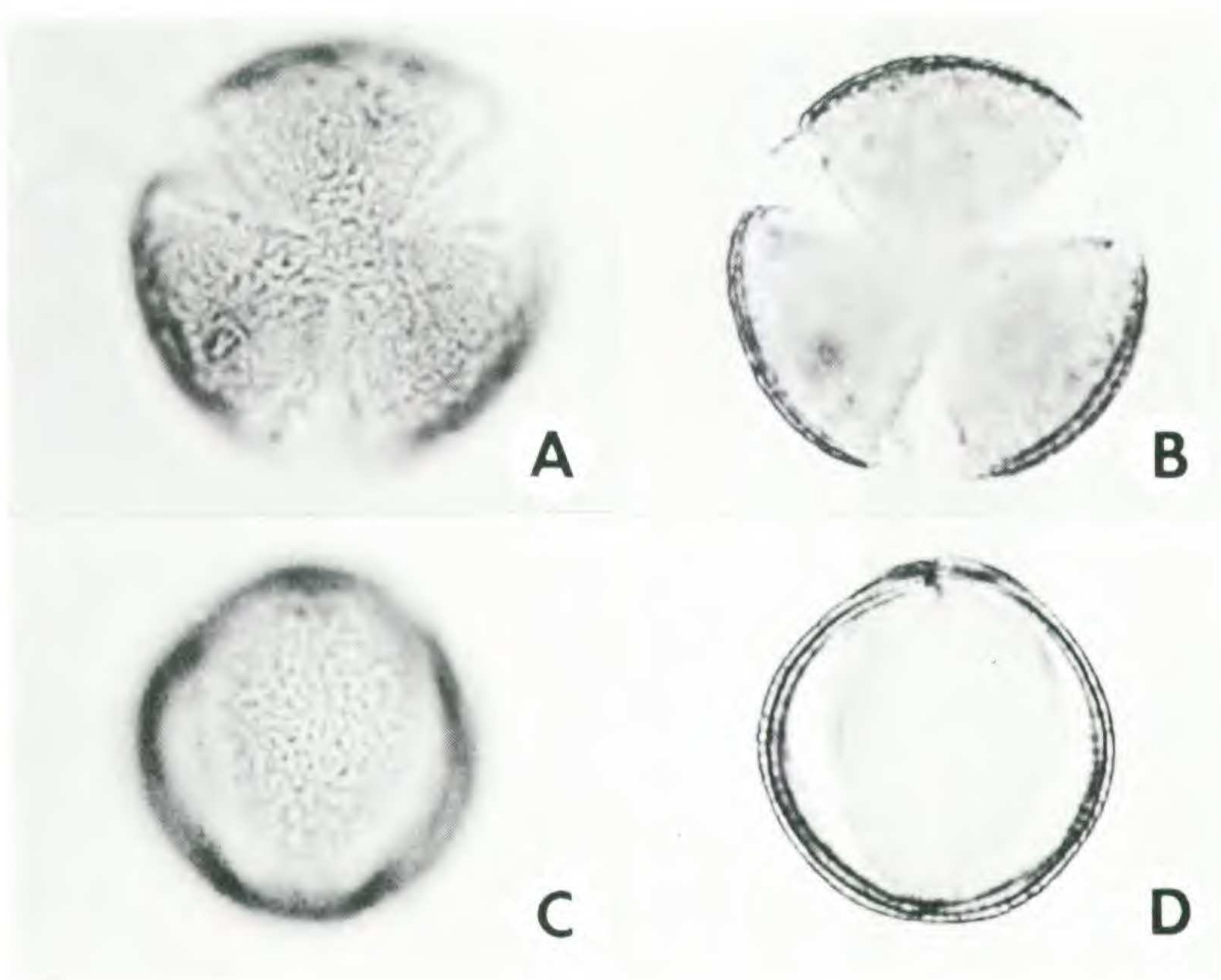
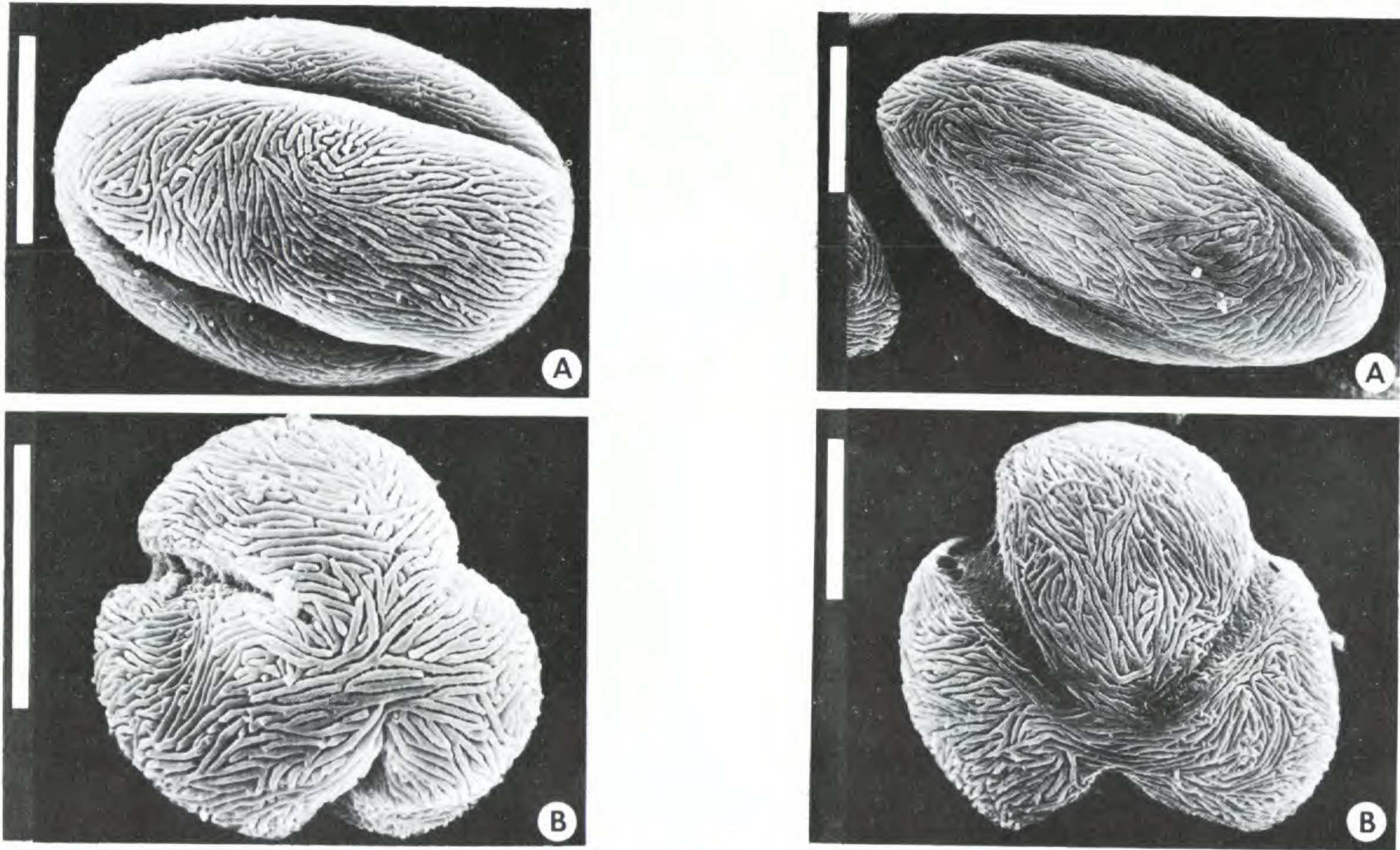
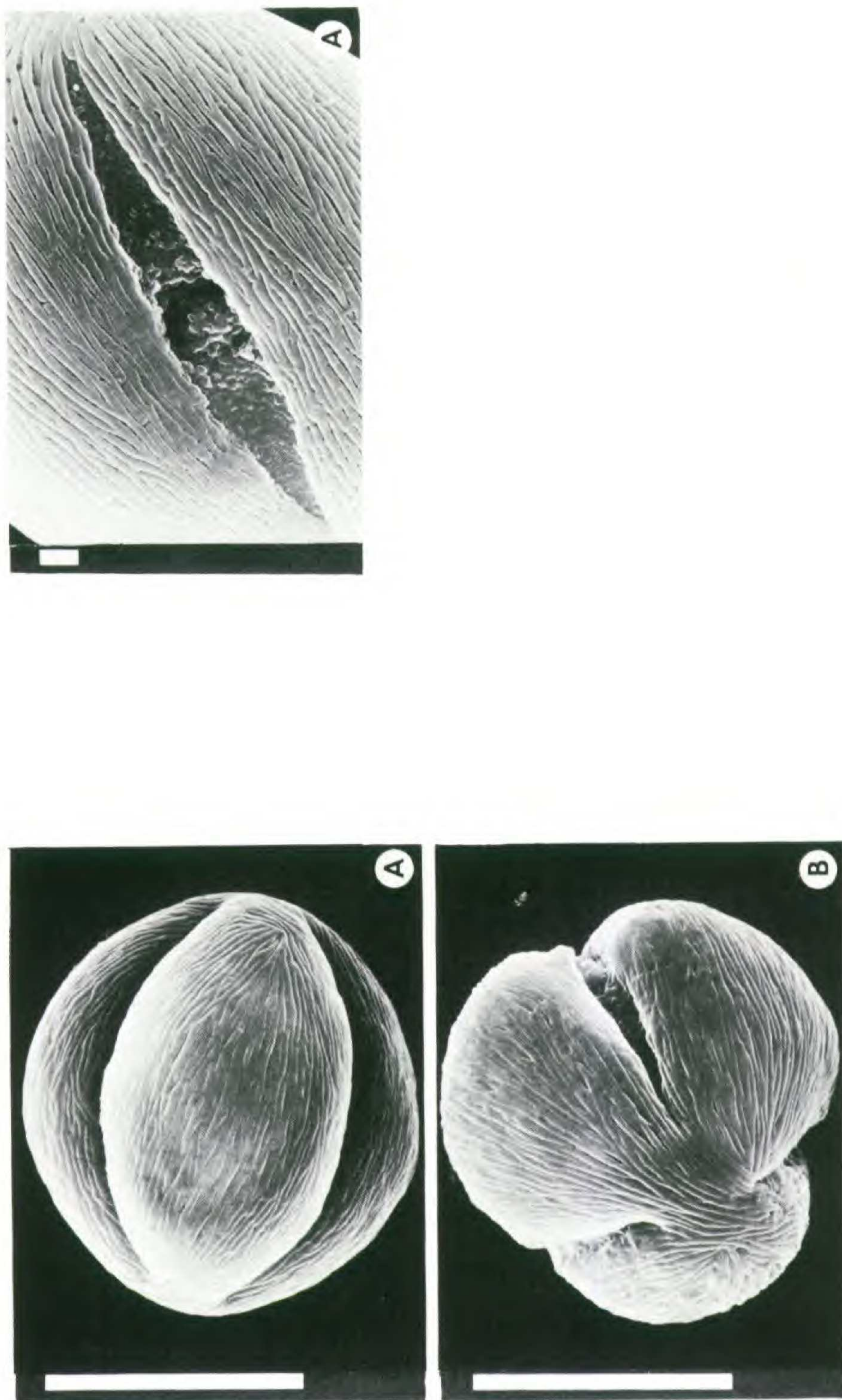


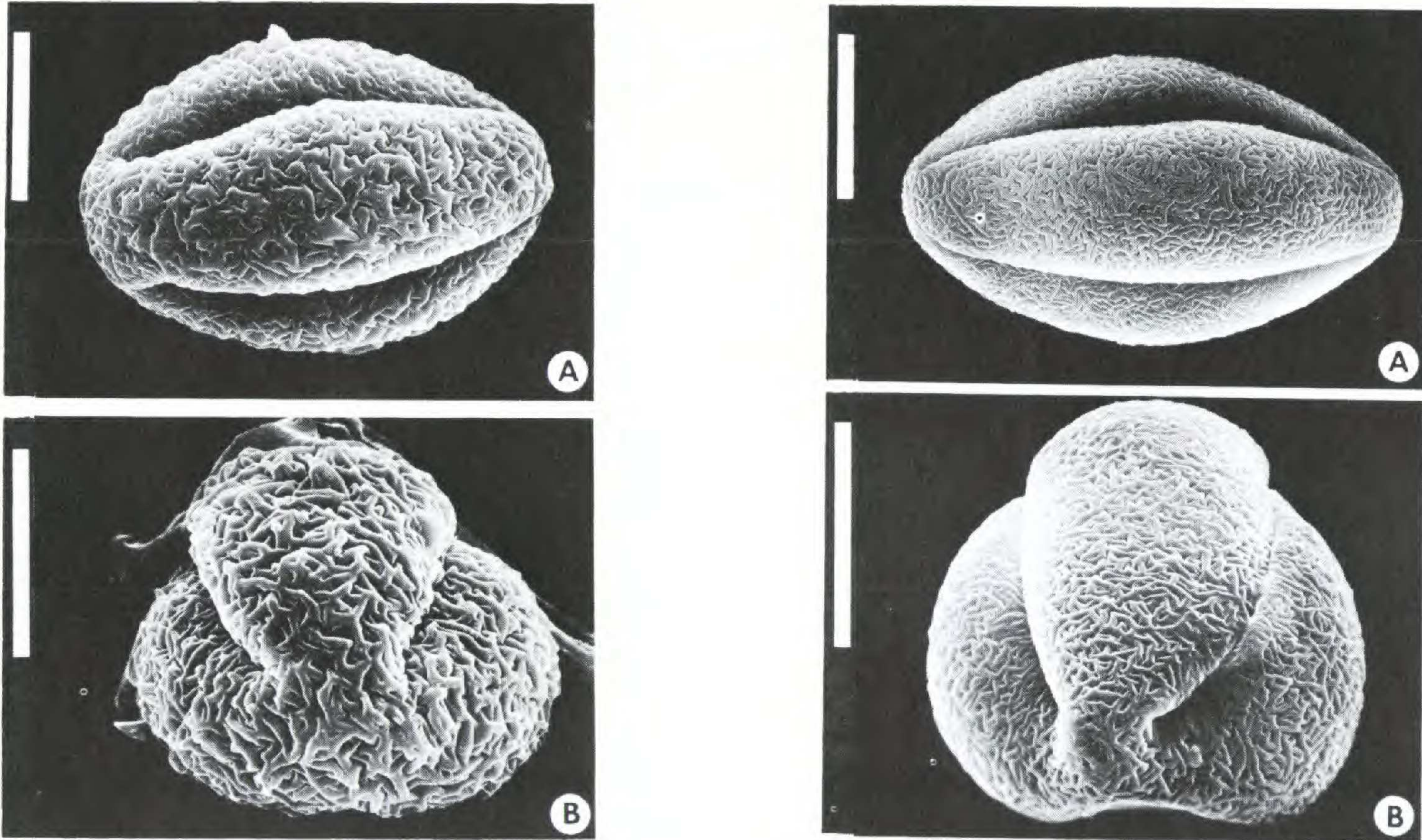
Figure 6. Light micrographs: A-D; *Acer nigrum*: **A**; Polar view, High focus, 1138X. **B**; Polar view, Mid focus, 1138X. **C**; Equatorial view, High focus, 1312X. **D**; Equatorial view, Mid focus, 1312X.



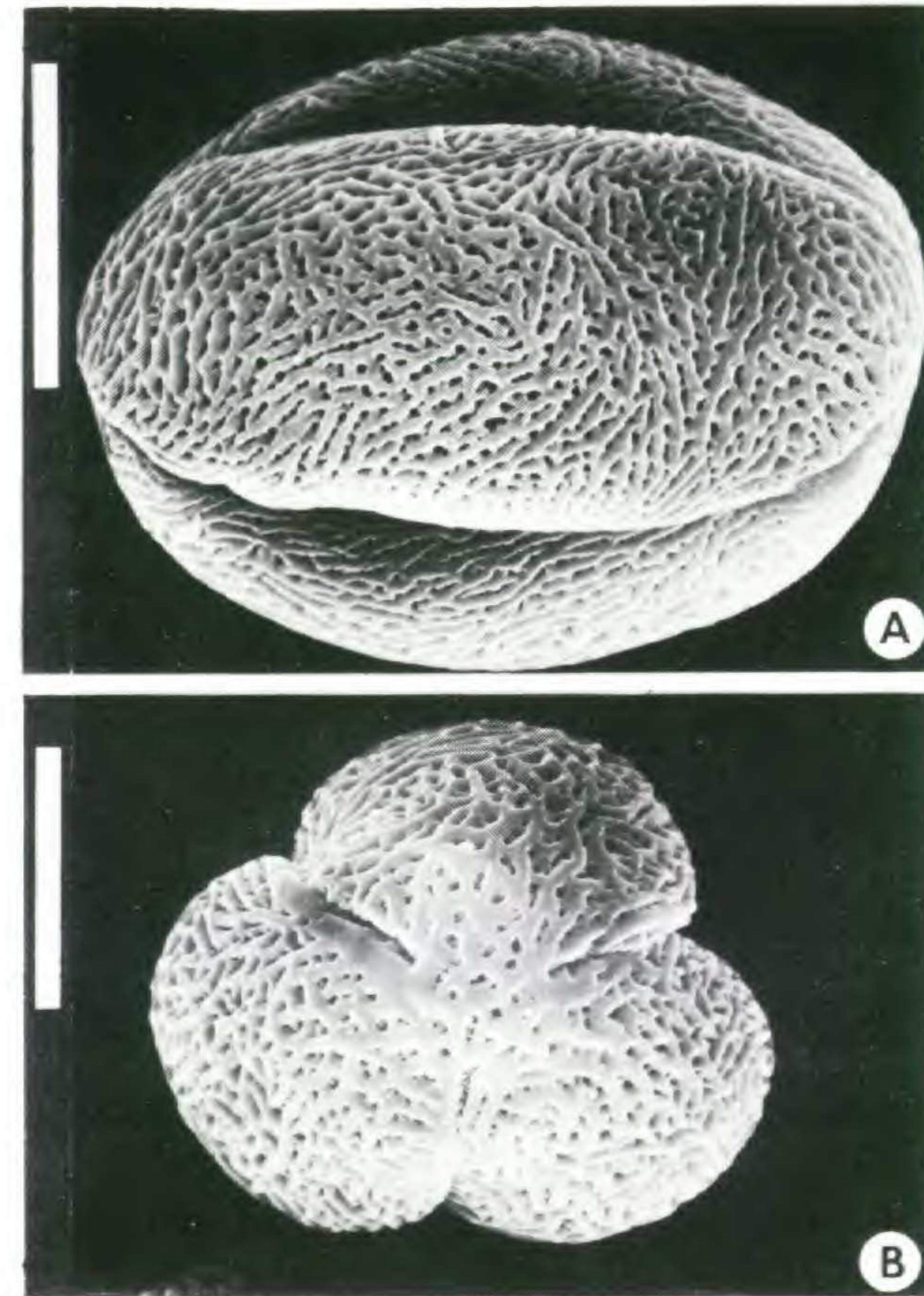
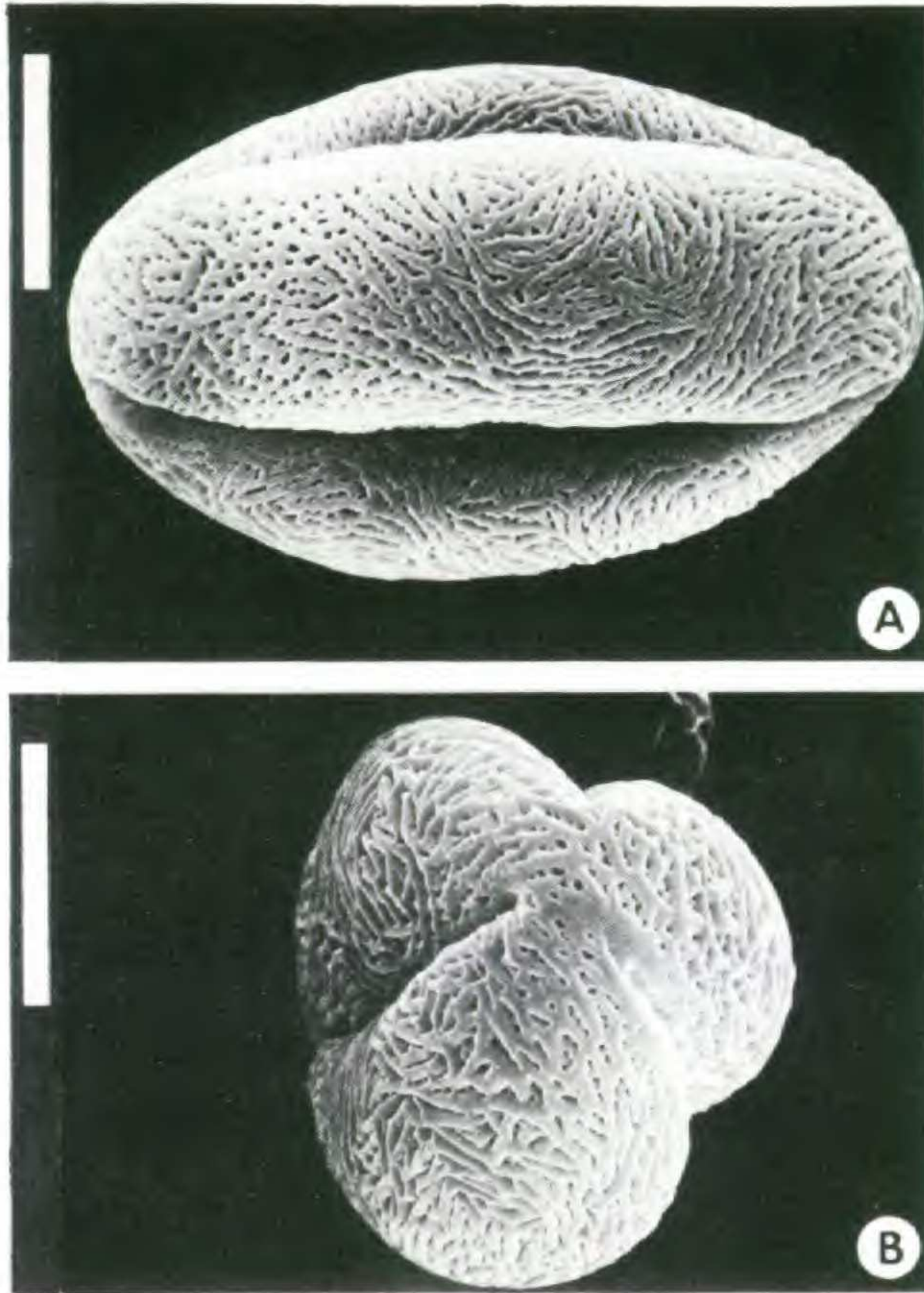
Figures 7 & 8. 7 (left). Scanning electron micrographs (Scale = $10\ \mu\text{m}$): A-B; *Acer pensylvanicum*: A; Equatorial view, showing fairly uniform width of lirae and striae. B; Slightly oblique polar view. 8 (right). Scanning electron micrographs (Scale = $10\ \mu\text{m}$): A-B; *Acer rubrum*: A; Equatorial view, showing lirae wider than striae and the $\pm$ continuous, interconnected striate nature. B; Slightly oblique polar view.



Figures 9 & 10. 9 (left). Scanning electron micrographs (Scale = 10 μ m): A-B; *Acer spicatum*: A; Equatorial view, showing "tight" orientation of the lirae. B; Slightly oblique polar view. 10 (right). Scanning electron micrograph (Scale = 1 μ m): A; *Acer spicatum*: Close-up of the equatorial region showing a colporate aperture.



Figures 11 & 12. 11 (left). Scanning electron micrographs (Scale = 10 μ m): A-B; *Acer negundo*: A; Equatorial view, showing rugulate sexine. B; Slightly oblique polar view, showing rugulate sexine. 12 (right). Scanning electron micrographs (Scale = 10 μ m): A-B; *Acer saccharinum*: A; Equatorial view, showing rugulate sexine. B; Slightly oblique polar view, showing rugulate sexine.



Figures 13 & 14. 13 (left). Scanning electron micrographs (Scale = 10 μ m): A-B; *Acer saccharum*: A; Equatorial view, showing striato-reticulate sexine. B; Slightly oblique polar view, showing striato-reticulate sexine. 14 (right). Scanning electron micrographs (Scale 10 μ m): A-B; *Acer nigrum*: A; Equatorial view, showing striato-reticulate sexine. B; Polar view, showing striato-reticulate sexine.

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